MORPHOLOGY AND PHYLOGENETIC SIGNIFICANCE OF THE ANGIOSPERM *PLATANITES HEBRIDICUS* FROM THE PALAEOCENE OF SCOTLAND

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ABSTRACT. Fossil platanoid leaves from the Palaeocene of Mull, north-west Scotland, are assigned to *Platanites hebridicus* Forbes. The leaves closely resemble those of extant Platanaceae, and differ only in being pinnately compound. Each leaf consists of a shallowly three-lobed terminal leaflet and two smaller asymmetric lateral leaflets. Reproductive structures associated with the fossil foliage are also similar to those of extant Platanaceae, and the only unequivocal differences are the ellipsoidal achene shape and the smaller number of achenes per fruiting head in the Palaeocene material. The combined information from leaves and reproductive structures establishes the '*P. hebridicus* plant' as one of the most completely understood fossil Platanaceae. The recognition of pinnately compound leaves in this critical angiosperm group has important implications for understanding the early divergence of major clades within the dicotyledons. During the mid-Cretaceous, simple, palmate platanoid leaves and pinnately compound *Sapindopsis* leaves exhibit partially intergrading patterns of venation and cuticular structure, and this has been used to suggest a close phylogenetic relationship between these early primitive representatives of the extant dicotyledonous subclasses Hamamelidae and Rosidae. The occurrence of extinct Platanaceae with compound leaves adds to the similarities between platanoid and *Sapindopsis* foliage, strengthens the proposed close relationship between the Platanaceae and Rosidae, and highlights the need to clarify relationships within the mid-Cretaceous platanoid-*Sapindopsis* complex.

THE extant family Platanaceae includes a single genus, *Platanus*, which consists of approximately nine species of temperate to tropical dicotyledonous trees (Li 1957; Ernst 1963) divided between two subgenera (Leroy 1982). Subgenus *Castaneophyllum* contains a single species, *P. kerrii* (Gagnepain 1939), that has unlobed elliptical leaves and occurs today only in tropical south-east Asia (Bůžek *et al.* 1967, 1976; Baas 1969; Kvaček 1970; Leroy 1982). *P. kerrii* is clearly distinct from all other species in the genus (Hsiao 1972, 1973). Subgenus *Platanus* contains approximately eight species with simple palmately lobed leaves, and has its centre of diversity in south-western North America, and Mexico. Two broadly distributed but disjunct species in subgenus *Platanus* are the familiar sycamore of eastern North America (*P. occidentalis*) and the plane tree of the eastern Mediterranean (*P. orientalis*).

Fossil leaves, inflorescences and infructescences very similar to those of extant Platanaceae first appear in the fossil record during the Albian (Lower Cretaceous) (Doyle and Hickey 1976; Hickey and Doyle 1977; Dilcher 1979; Crane *et al.* 1986; Upchurch and Wolfe 1987; Crane, in press *a*; Friis *et al.* in press; Schwarzwalder and Dilcher, in press). *Platanus*-like plants are therefore known very early in the initial diversification of non-magnoliid ('higher') dicotyledons, which are characterized by tricolpate or tricolpate-derived pollen (subclasses Asteridae, Caryophyllidae, Dilleniidae, Hamamelidae, Ranunculidae, Rosidae, *sensu* Takhtajan, 1980). Subsequently platanaceous leaves are common constituents of middle to high latitude fossil floras in the late Cretaceous and Tertiary of the Northern Hemisphere (Crane 1987; Manchester 1986; Upchurch and Wolfe 1987). The variety of foliar morphology among fossil Platanaceae strongly suggests that extant *Platanus* reflects only a small proportion of the total diversity of the platanaceous clade, and this is supported by the morphological variety among platanoid inflorescences and infructescences

recently reported from the Cretaceous and early Tertiary (Friis 1984, 1985b; Crane *et al.* 1986; Manchester 1986; Crane, in press *a*; Friis *et al.*, in press). In this paper we describe unusual compound platanaceous leaves (*Platanites hebridicus* Forbes) and associated reproductive structures from the Palaeocene of Mull, north-west Scotland. We suggest that these different isolated organs were produced by a single extinct species. The combined information establishes *P. hebridicus* as one of the more completely understood fossil Platanaceae and permits a detailed assessment of its similarities to Recent species.

MATERIAL AND METHODS

Plant fossils from the interbasaltic sediments of Mull were first described by Forbes (1851). They have since been the focus of several palaeobotanical studies, and additional plant fossil localities have been discovered in other parts of north-west Scotland (Gardner and Ettingshausen 1879–1882; Gardner 1883–1886, 1887; Edwards 1923; Seward and Holttum 1924; Johnson 1933, 1934, 1935, 1936, 1937; Seward 1939; Crane, in press *b*). The Mull flora is dominated by angiosperm leaves: fruits, seeds, and other reproductive structures are rare in the collections currently available.

All of the specimens considered in this study are from the classic interbasaltic 'leaf beds' (Argyll 1851; Gardner 1887) on the Ardtun peninsula near Bunessan in south-western Mull (National Grid Reference NM 377247). At least two different localities and two different stratigraphic levels on the Ardtun peninsula have yielded *Platanites* leaves (Gardner 1887), but the exact provenance of individual specimens is unknown. The maximum igneous activity in north-west Scotland is dated as early Palaeocene, between 66–58 million years before present (Curry *et al.* 1978). Palynological assemblages from Mull and other localities in this area have received considerable attention (Simpson 1937, 1961; Martin 1968; Phillips 1974; Srivastava 1975) and the most recent palynological assessments (Curry *et al.* 1978), which suggest an early Palaeocene age, are in broad agreement with the radiometric data.

We have examined specimens from Ardtun in the British Geological Survey, Edinburgh and Keyworth; the Cockburn Museum, University of Edinburgh; the Royal Scottish Museum, Edinburgh; the Hunterian Museum, Glasgow; the British Museum (Natural History), London; the City Museum and Art Gallery, Glasgow. The most informative specimens, and all of the material cited and illustrated in this paper have either a 'V' prefix and are in the collections of the Department of Palaeontology, British Museum (Natural History), or a BGS prefix and are in the collections of the British Geological Survey, Keyworth, Nottinghamshire. Carbonaceous fragments from the staminate inflorescence were cleaned in hydrofluoric acid and macerated in concentrated nitric acid followed by ammonia to yield pollen for light and scanning electron microscopy. Terminology of leaf architectural features follows Hickey (1973). Annotations of the synonymy list follow the recommendations of Matthews (1973).

SYSTEMATIC PALAEONTOLOGY

Division MAGNOLIOPHYTA Cronquist, Takhtajan and Zimmermann, 1966
Class MAGNOLIOPSIDA Cronquist, Takhtajan and Zimmermann, 1966
Subclass HAMAMELIDAE Takhtajan, 1966
Family PLATANACEAE Dumortier, 1829

FOLIAGE

Genus PLATANITES Forbes, 1851

Type species. Platanites hebridicus Forbes, 1851.

Generic diagnosis. Leaves compound with a trilobed terminal leaflet and a pair of ovate, asymmetrical lateral leaflets. Terminal leaflet with three palinactinodromous primary veins; lateral leaflets with a single primary vein. Secondary venation of both terminal and lateral leaflets pinnate and craspedodromous with the veins ending in teeth. Tertiary venation percurrent, at right angles to the secondary veins.

Remarks. No formal diagnosis was provided by Forbes and the specimens figured as *P. hebridicus* (Forbes 1851, pl. 3, fig. 5; pl. 4, fig. 1) are fragments of two terminal leaflets, and do not show the compound morphology of the complete leaf. However, there is no evidence of more than one taxon of *Platanus*-like leaves at the Ardtun locality, and all specimens in which the leaf rachis is complete have either attached lateral leaflets (text-figs. 1A, B, F and 2B, C) or distinct leaflet scars (text-fig. 1D, H). This feature is the major character separating leaves of *Platanites* from those of extant *Platanus*, and it is therefore incorporated in the generic diagnosis. Our revised concept of *Platanites* will not accommodate simple platanoid leaves that differ in other respects from those of extant *Platanus*. Fossil wood assigned to this genus (Mathiesen 1932) must also be excluded. Several fossil angiosperm leaves illustrated in the literature, previously assigned to other genera, now fall within our circumscription of *Platanites*. These include some of the specimens previously assigned to *Negundo fremontensis* Berry (Berry 1931, pl. 11, figs. 1–3), *N. decurrens* Lesquereux (Knowlton 1930, pl. 45, fig. 10), and *Platanus guillelmae* Göppert (Knowlton 1930, pl. 33, fig. 2) from the uppermost Cretaceous or Palaeocene Denver Formation of Colorado, and *Cissus marginata* (Lesquereux) Brown (Brown 1962, pl. 53, fig. 4; pl. 54, figs. 3 and 4) from the Palaeocene, Fort Union Formation of Montana and the Middle Eocene of northwestern Wyoming (MacGinitie 1974). In the absence of a detailed investigation of the original material of these species, the necessary new combinations are not formally proposed in this paper.

Platanites hebridicus Forbes, 1851

Text-figs. 1A–H, 2A–C, 4A

v* 1851   *Platanites hebridicus* Forbes, p.103, pl. 3, fig. 5; pl. 4, fig. 1 (also pl. 4, fig. 2, and possibly pl. 3, fig. 1, both listed as 'affinities doubtful').
    1856   *Platanites hebridicus* Forbes; De La Harpe, p. 136.
    1886   *Platanites aceroides* Gardner, p. 104.
v   1887   *Platanites hebridicus* Forbes; Gardner, pp. 289, 290, 296, pl. 13, figs. 4, 12–14a.
    1924   *Platanus hebridica* (Forbes); Seward and Holltum, p. 83, fig. 14.
    1937   *Hamamelis suborbiculata* Johnson, p. 317, pl. 20, fig. 4 (lateral leaflet).

Specific diagnosis. Terminal leaflet broad, length to width ratio approximately 1:1. Apex acute, base typically broadly cuneate. Sinuses between lobes shallow. Lateral primary veins of terminal leaflet diverging alternately above the base of the lamina at acute angles. Secondary veins diverging from the primary veins at angles of 40–65° and terminating in well-developed teeth. Other teeth supplied by strong tertiary veins that arise abmedially from the supra-adjacent secondary vein. Lateral leaflets smaller than the terminal leaflet, subsessile and subopposite on the rachis; attached well above the base of the rachis and well below the terminal leaflet. Lamina of lateral leaflets prominently expanded along the side closest to the base of the leaf, the expansion sometimes forming a discrete lobe supplied by a strongly developed basal secondary vein. Teeth of both terminal and lateral leaflets simple; usually asymmetric with the upper margin concave and the lower margin convex.

Lectotype. BGS GSM 76599 (Forbes 1851, pl. 3, fig. 5).

Syntypes. BGS GSM 77352 (Forbes 1851, pl. 4, fig. 1), 77353 (Forbes 1851, pl. 4, fig. 2).

Other material. V.2479, 24977, V.25031, V.25034, V.25035, V.25036, V.25039–25041, V.25061, V.25064, V.25065, V.25068, V.25089, V.25206, V.25237.

Locality. Ardtun peninsula, 3 km north of Bunessan, Mull, Scotland. National Grid Reference NM 377247.

Stratigraphy. 'Ardtun Leaf Beds', probably early Palaeocene.

Description. At least six specimens illustrate that the leaves of *Platanites hebridicus* are compound (text-figs. 1A, B, F and 2B, C) and this unusual feature was first noted by Seward and Edwards (unpublished manuscript BM(NH)). The two lateral leaflets are attached sub-oppositely to the rachis, 2 to 6 cm below the terminal leaflet and 3·5–7·5 cm above the base of the rachis. The rachis may be up to about 10 cm long.

TEXT-FIG. 1. *Platanites hebridicus* Forbes, leaf morphology. A, compound leaf showing large terminal leaflet, long rachis, and a single lateral leaflet, V.25040, ×0·35. B, compound leaf showing large terminal leaflet, and partially superimposed lobed lateral leaflet, V.25031, ×0·3. C, detail of intercostal venation of terminal leaflet in H, showing percurrent tertiary veins and quaternary venation, ×0·85. D, detail of rachis of terminal leaflet in H showing the subopposite scars of two lateral leaflets, ×1. E, detail of base of terminal leaflet in H showing venation of basal margin; note strongly palinactinodromous primary veins, ×0·85. F, leaf rachis showing the base of a terminal leaflet and two complete lateral leaflets; note maximum development of lamina directed toward the leaf base, V.25061, ×0·5. G, detail of lateral leaflet margin in F showing venation and marginal teeth, ×1. H, terminal leaflet of a compound leaf; note two scars toward the base of the leaf rachis, V.25039, ×0·35.

Terminal leaflets are slightly asymmetric, broadly trilobed, and are about 18–24 cm long and 16–28 cm wide based on estimates from the most complete specimens. Johnson (1933) mentions a specimen 37 cm long. Often terminal leaflets are wider than they are long. They have palinactinodromous venation (text-figs. 1A, B, H and 2A), with the lateral primary veins diverging alternately from the midvein at angles of 40–65° (text-fig. 1E). The lowermost primary vein may diverge very close to the base of the lamina (text-figs. 1A and 2A) or several millimetres above the base of the leaflet (text-fig. 1E). The points of divergence of the secondary veins are usually several millimetres apart. The lobes of the terminal leaflet are broad and sinuses shallow such that the distance from the leaflet base to the sinus is about two-thirds of the distance from the base to the apex. None of the specimens clearly show the leaf apex although the form of the lamina indicates that it is acute (text-fig. 2A). The base of the terminal leaflet is broadly cuneate, frequently slightly asymmetric, and forms an angle of approximately 75–140°.

The lateral leaflets are more or less sessile or with a short petiolule up to 5 mm long. In some specimens they are detached, leaving prominent scars on the rachis (text-fig. 1D, H). Isolated lateral leaflets (Forbes 1851, pl. 4, fig. 2; Johnson 1937, pl. 20, fig. 4; Phillips 1974, pl. 1, fig. 1) are easily recognized by their asymmetry and pinnate venation (text-fig. 2B, C). They are broadly ovate but distinctly asymmetric with the maximum development of the lamina on the side closest to the base of the leaf. Occasionally the expanded portion of the lamina forms a weakly developed lobe supplied by a prominent secondary vein (text-fig. 2C). The sinus formed by the lobe is very shallow. Lateral leaflets are about 40–120 mm long and 35–90 mm wide. The apex of the leaflet is acute and the base obtuse to truncate.

In both terminal and lateral leaflets there are four to eight pairs of secondary veins which arise alternately from the midvein at angles of about 40–65°. Secondary veins are craspedodromous, slightly admedially curved, and terminate in prominent teeth. Tertiary veins are percurrent, typically straight, occasionally branched (text-fig. 1C) and arise from the secondary veins at approximately 90° with intervals of 5–10 mm. Higher order venation is orthogonal with quaternary veins arising approximately at right angles and typically delimiting two rows of more or less isodiametric areolae between each pair of tertiary veins. Teeth are simple, obtuse or occasionally glandular, with a concave upper flank and convex lower flank (text-fig. 1G). Each tooth is supplied either directly by a secondary vein or by an abmedial branch from the supra-adjacent secondary vein. In both terminal and lateral leaflets, teeth toward the base of the lamina are supplied by strongly developed tertiary veins derived admedially from the lowermost secondary (text-fig. 1F). The vein is positioned medially in each tooth. Cuticular details have not been obtained from any of the specimens.

## ASSOCIATED REPRODUCTIVE STRUCTURES

Infructescences and fruits

Description. An isolated fruiting head from Mull was illustrated by Gardner (1887, pl. 13, fig. 12). Heads are 10–17 mm in diameter, but there are no specimens that show whether they were originally sessile along an infructescence axis or other details of how they were borne. Compressed heads show approximately forty curved styles protruding from the periphery (text-fig. 2D, E), and we estimate that each head probably contained approximately 200–300 achenes. Floral details are not preserved, and the number of carpels per flower cannot be determined. Isolated achenes are typically 6–7 mm long and consist of a slender elliptical body and an apical elongated, curved persistent style (text-fig. 2F). The body is about 4 mm long and 2 mm wide, and the style typically 1–2 mm long. No hairs have been observed associated either with the infructescences or the dispersed achenes, although it is possible that they were present and not preserved.

Material. V.25052, V.25057, V25058, V.62186.

Staminate Inflorescences

Description. Staminate infloresences are more common in the Mull assemblage than infructescences (Gardner 1887, p. 290) and several specimens have been illustrated previously (Gardner 1887, pl. 13, figs. 11, 13, 14, 14a, 15; Phillips 1974, pl. 1, fig. 3). They consist of spherical heads that are borne on short stalks up to 3 mm long, distributed along elongated inflorescence axes. The heads are typically 5 mm apart and the most complete specimen shows the positions of at least six (possibly nine) heads borne along a single inflorescence axis (text-fig. 3A). Heads are 6–11 mm in diameter and the surface consists of polygonal areas approximately 0·5 mm in diameter formed by the distally expanded connective of the stamens (text-fig. 2D). We estimate that each head contained about 300 stamens. Floral details, including the number and arrangement of stamens per flower, are unknown, although fragmentary staminate heads (text-fig. 3C) show short persistent
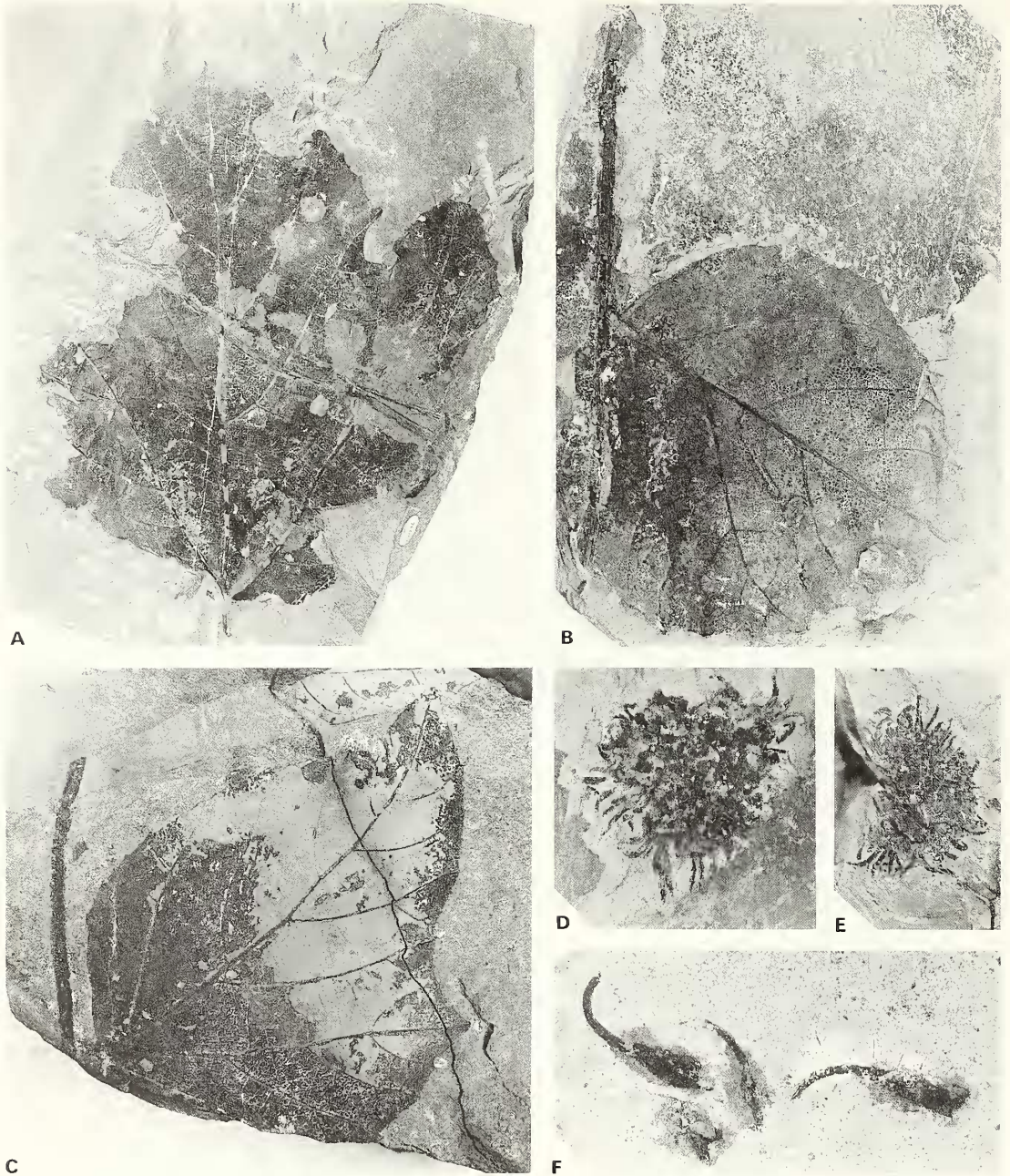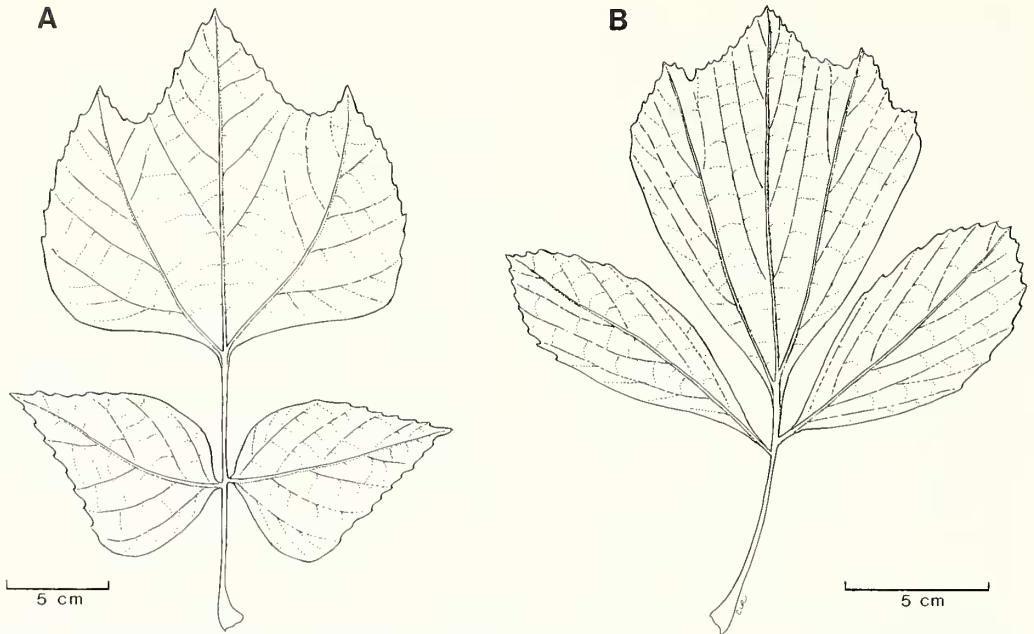
TEXT-FIG. 2. *Platanites hebridicus* Forbes, leaf morphology and associated infructescences and fruits. A, terminal leaflet, V.25036, ×0·5. B, leaf rachis showing attached asymmetrical lateral leaflet, V.2479, ×1. C, leaf rachis showing asymmetrical lateral leaflet with two lobes separated by a shallow sinus, V.25064, ×1. D, infructescence showing numerous projecting styles, V.25052, ×2·5. E, infructescence showing numerous projecting styles, V.62186, ×2·5. F, four dispersed achenes with curved elongated styles at the apex, V.25058, ×4.
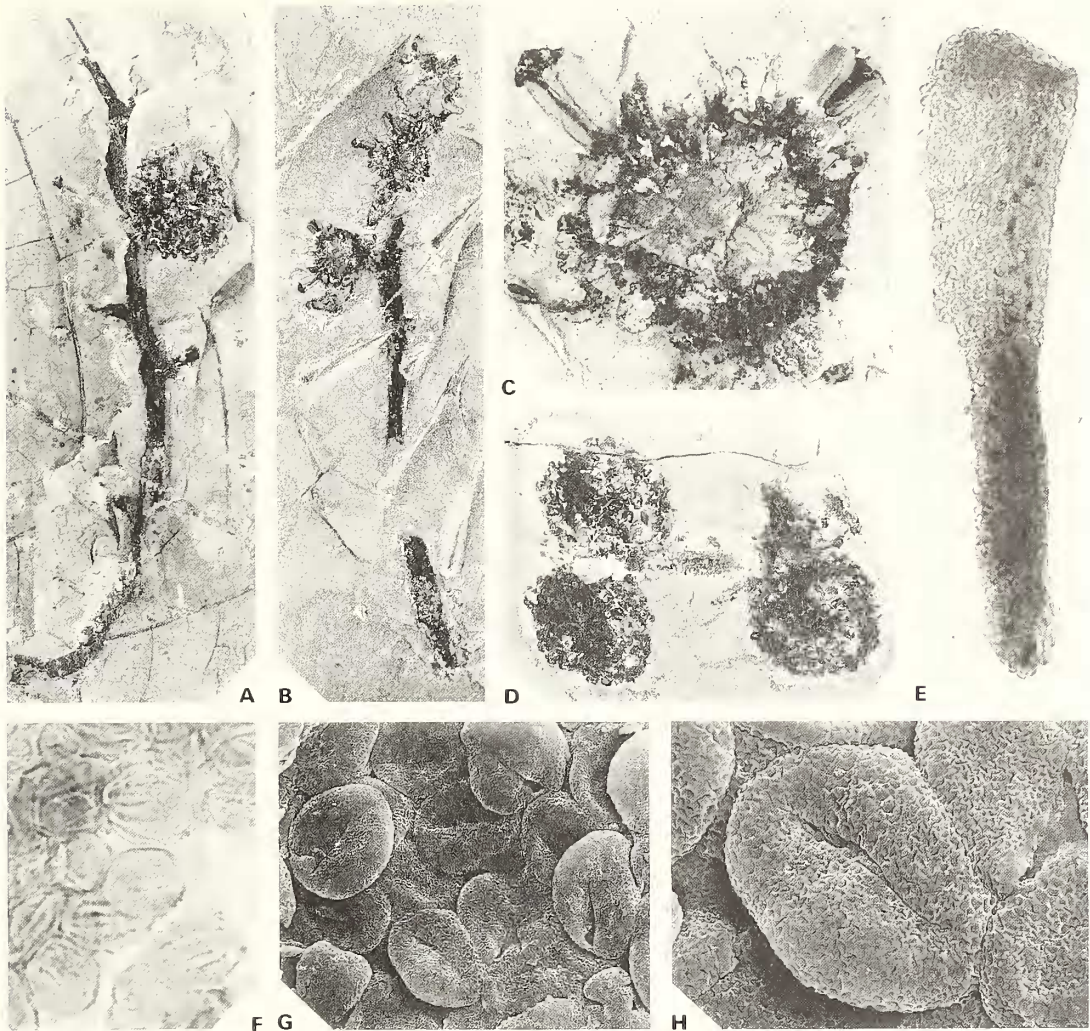
TEXT-FIG. 3. Staminate inflorescences and pollen associated with *Platanites hebridicus* Forbes. A, staminate inflorescence showing a single staminate head and the attachment points of five (possibly eight) other staminate heads, V.25054, × 2. B, staminate inflorescence showing three attached staminate heads, V.25051, × 2. C, detail of staminate head showing two attached anthers; note the distally expanded peltate connective, short filaments, and short persistent perianth parts, V.25051, × 10. D, staminate inflorescence with four attached heads, V.25055, × 3. E, contents of a single pollen sac isolated from staminate head in D, × 100. F, light micrograph of pollen isolated from staminate head in D, × 750. G, SEM of several pollen grains isolated from staminate head in D, showing equatorial and polar views, × 1000. H, SEM of pollen grain isolated from staminate head in D, equatorial view showing colpus and microreticulate-rugulate tectum in mesocolpial areas, × 2500.

perianth parts. Stamens were shed individually (Gardner 1887, pl. 13, fig. 14) and consist of a short filament, elongate anthers typically 0·8 mm long and a short capitate connective (text-fig. 3C). Pollen isolated from organically preserved staminate heads is prolate, 16–20 μm in polar length, tricolpate, and very finely microreticulate (text-fig. 3F–H). Exine sculpture resembles that of the dispersed pollen species *Tricolpites dubhensis* S. K. Srivastava isolated from the Shiaba lignite on Mull which is approximately contemporaneous

A   **B**

TEXT-FIG. 4. Reconstructions of compound platanoid leaves. A, *Platanites hebridicus* Forbes; based on specimens illustrated in text-figs. 1 and 2. B, '*Cissus*' *marginata* (Lesquereux) Brown; based on Brown (1962, pl. 53, fig. 4; pl. 54, fig. 4).

with the Ardtun leaf beds (Simpson 1961; Srivastava 1975). Both the pollen isolated from the fossil staminate inflorescences and the holotype of *T. dubhensis* (Srivastava 1975, pl. 12, figs. 1 and 2) have muri that are approximately triangular in cross-section as in pollen of extant *Platanus* (e.g. Hesse 1978; Zavada and Dilcher 1986). The grains described here differ from *T. dubhensis* only in having a smaller polar length (16–20 μm vs. 20–30 μm).

Material. V.14850, V.25003, V.25051, V.25053–25056, V.25060, V.25221.

DISCUSSION

We have no direct evidence of attachment that conclusively links *Platanites hebridicus* with the associated infructescences and staminate infructescences, and we therefore do not formally assign the leaves and reproductive structures to the same species. However, each dispersed organ can be assigned to the Platanaceae on independent evidence, and in all of the Mull material examined we found no other plant fossils referable to this family. *P. hebridicus* is one of the more common leaves in the Ardtun flora, and together with the absence of other platanaceous fossils this makes it likely that the fossil leaves, inflorescences, and infructescences were produced by a single species. If this is accepted, then the combined information from different organs permits a more useful comparison of the Mull species with other fossil and extant Platanaceae.

Comparison with extant Platanaceae

In all features of morphology and venation the terminal leaflets of *Platanites hebridicus* closely resemble the simple leaves of extant *Platanus* subgenus *Platanus*, such as those of *P. occidentalis*. Lateral leaflets do not occur in any extant *Platanus* species (Jaennicke 1899; Brown 1962; Depape and Brice 1966), but elaborately developed stipules may be present both in extant and fossil *Platanus* (Crane 1981; Leroy 1982; Schwarzwalder and Dilcher in press). These stipules have

been considered homologous to the basilaminar expansions seen in the leaves of some extant and fossil *Platanus* species (Ward 1888) but could also be interpreted as homologous to the leaflets of *Platanites* and similar taxa.

The arrangement of staminate flowers and the morphology of stamens is typical of that seen in extant *Platanus*. The stamens are aggregated into more or less spherical heads, and have a characteristic short, domed apical extension of the connective (Boothroyd 1930). The tricolpate microreticulate pollen is also similar to that in extant *Platanus*. Pollen size (16–20 μm) is close to the range typical of subgenus *Castaneophyllum* (16–18 μm) and smaller than is typical of subgenus *Platanus* (20–25 μm) (Ludlow-Wiechers and Nieto 1982; Manchester 1986; Zavada and Dilcher 1986). The arrangement of sessile staminate heads along the fossil inflorescences is also similar to that in extant *Platanus*. The number of staminate heads per inflorescence is intermediate between the one to five heads seen in subgenus *Platanus* and the numerous (> 20) heads seen in subgenus *Castaneophyllum*.

The diameter of the fruiting heads is smaller than is typical of subgenus *Platanus* and more like that in subgenus *Castaneophyllum*. Each fruiting head is much less compact than in both extant subgenera. Details of floral structure are not preserved in the Mull material, but there is no evidence in the compressed heads that the fruits are clustered into discrete floral units. In some fossil species (Friis 1985*b*, Manchester 1986; Friis *et al.* in press) there are prominent perianth parts and compressed fruiting heads clearly show discrete clusters of fruits. By comparison with extant *Platanus*, the fruits in the fossil material are interpreted as achenes. Fruit shape differs from that of all extant species in being narrowly ellipsoidal rather than obovoid. We cannot determine whether the apparent absence of hairs on the fossil fruits is original or the result of poor preservation. Abundant hairs typically develop from the base of the fruit wall in extant *Platanus*. However, well-preserved fossil material indicates that these hairs were absent in some extinct taxa (Manchester 1986).

Comparison with other fossil Platanaceae

The recognition that *Platanites hebridicus* has compound leaves clearly invalidates the early comparisons made by Heer (1856) with taxa with simple leaves (*Platanus aceroides* Göppert, *P. guillelmae* Göppert). However, although this is the first unequivocal demonstration of pinnately compound leaves in Platanaceae, specimens of five other platanoid species from the uppermost Cretaceous or early Tertiary of North America have been illustrated previously that resemble *Platanites hebridicus* in this respect. A single specimen of *Platanus appendiculata* Lesquereux from the early Eocene (MacGinitie, *pers. comm.*; Wolfe, *pers. comm.*) of the Sierra Nevada (Lesquereux 1878, pl. 3, fig. 3) shows two lateral laminae attached to the leaf rachis, but because these occur at the base of the leaf rachis or petiole, it is uncertain whether they are lateral leaflets or a pair of basal stipules. MacGinitie (1941) collected no further specimens that showed this feature and considered it to be of little systematic significance in his revision of the Sierra Nevada flora.

Negundo fremontensis Berry (1931, pl. 11, figs. 1–3) from the Middle Eocene of the Wind River Basin, Wyoming is only known from isolated terminal and lateral leaflets but Berry's reconstruction (1931, text-fig. 6) based on field association is closely similar to *P. hebridicus*. In particular the shape of the lateral and terminal leaflets is almost identical to that in *P. hebridicus*, and re-examination of the original material from Wyoming may demonstrate that '*N*'. *fremontensis* and *P. hebridicus* are conspecific. '*N*'. *fremontensis* was assigned to *Aleurites* (Euphorbiaceae) by MacGinitie (1974).

The holotype, and only specimen, of *N. decurrens* Lesquereux (1889, p. 54), illustrated by Knowlton (1930, pl. 45, fig. 10; Museum of Comparative Zoology, Harvard, no. 1523) from the uppermost Cretaceous or earliest Palaeocene of the Denver Basin was regarded by Brown (1962) as conspecific with a specimen of *Platanus guillelmae* Göppert illustrated from the same flora (Knowlton 1930, pl. 33, fig. 2). The holotype shows part of a poorly preserved probable lateral leaflet adjacent to the rachis of a platanoid leaf. Brown (1962) placed both of these specimens and the single specimen assigned to the fossil taxon *Winchellia triphylla* Lesquereux (1893, pl. 8, fig. 1)

in the species *Cissus marginata* (Lesquereux) Brown. Brown illustrated three specimens of *C. marginata* from the Palaeocene Fort Union Formation of western North America that show the compound nature of this leaf (1962, pl. 53, fig. 4; pl. 54, figs. 3 and 4; see also Dorf 1942, pl. 17, fig. 4), and a similar specimen is reported from the Middle Eocene of north-western Wyoming by MacGinitie, who noted the similarities to leaves of extant *Platanus* (1974, pl. 14, fig. 1). Other compound platanoid leaves occur in the Palaeocene Ravenscrag Formation of southern Saskatchewan (Basinger *pers. comm.*). With the exception of '*N*' *fremontensis* (Berry 1931) all of these specimens differ from *Platanites hebridicus* in having a terminal leaflet with a more acute base that is frequently decurrent along the leaf rachis (text-fig. 4B). The specimens of '*C. marginata*' also have more symmetrical lateral leaflets than those of *P. hebridicus*. Although the reproductive structures of '*C. marginata*' are unknown, there may have been several species of Platanaceae with compound leaves during the early Tertiary.

Although fossil Platanaceae are abundant in the mid-Cretaceous none of these taxa have so far been reconstructed in detail. Isolated mid-Cretaceous reproductive structures differ from those associated with *P. hebridicus* in having more numerous smaller heads borne along the infructescence axis, more prominent perianth parts, smaller pollen, and usually stamens with a more elongated apical extension of the connective (Dilcher 1979; Friis 1985b; Crane *et al.* 1986; Friis, Crane and Pedersen, in press).

The most completely reconstructed species of extinct Platanaceae is the plant which bore the leaves *Macginitiea angustiloba* (Lesquereux) Manchester (1986) from the Middle to late Eocene of Oregon. The leaves of *M. angustiloba* differ from those of *P. hebridicus* in being simple and having five to seven palmately arranged lobes. However, there are some similarities in the associated reproductive structures. Both species differ from extant *Platanus* in having ellipsoidal achenes, with a persistent elongated style, that apparently lacks a mass of dense hairs at the base. The '*M. angustiloba* plant' and the '*P. hebridicus* plant' differ in the aggregation of *Macginitiea* achenes (*Macginicarpa*) into clusters of five surrounded by prominent perianth parts, the tendency of *Macginitiea* stamens (*Macginistemon*) to adhere together in groups of five by hairs arising from an elongated apical extension of the connective (Manchester 1986) and the smaller pollen size in *Macginistemon* (11–16 μm).

In summary, *P. hebridicus* possesses a mosaic of characters that is unique among fossil and extant Platanaceae. Although some, probably derived, features, e.g., the shape of the expanded connective and pollen size, are indicative of a close relationship to extant Platanaceae, other characters such as ellipsoidal achenes, elongated inflorescences with several heads of flowers, may be generalized characters within the platanaceous clade.

Evolution of the Platanaceae

Fossil leaves with the architectural features of extant Platanaceae first appear in the mid–late Albian (Lower Cretaceous) and provide some of the earliest evidence of the dicotyledonous subclass Hamamelidae (Wolfe *et al.* 1975; Doyle and Hickey 1976; Hickey and Doyle 1977; Upchurch and Wolfe 1987; Crane, in press *a*). This early platanoid foliage exhibits considerable morphological variation and had previously been assigned to several extant genera in different families (e.g. *Aralia, Sassafras, Sterculia*, Lesquereux 1892; Berry 1902, 1903; Seward 1927; Schwarzwalder 1984, 1986; Schwarzwalder and Dilcher, in press). Fossil platanaceous wood is also known from the late Albian (Cedar Mountain Formation, Utah), although its structure is rather generalized and it does not show certain specialized features, such as simple perforation plates, that occur in the wood of the extant genus (Tidwell, *pers. comm.*, and *pers. observ.*). In the late Cretaceous and early Tertiary platanoid foliage is diverse and widely distributed in fossil floras from the Northern Hemisphere (e.g. Ward 1888, 1890; Berry 1914; Depape and Brice 1966; MacGinitie 1969; Knappe and Rüffle 1975, Němejc and Kvaček 1975; Walther 1985; Wolfe and Wehr 1987), and the abundant record of leaves is paralleled by numerous reports of fossil wood (e.g. Felix 1896; Prakash and Barghoorn 1961; Prakash *et al.* 1971; Page 1968; Süss 1971, 1980; Brett 1972; Süss and Müller-Stoll 1975, 1977; Wheeler *et al.* 1977; Mai and Walther 1978; Scott and Wheeler 1982; Manchester 1986).

The fossil record of platanaceous reproductive structures is also extensive and is receiving increasing attention (Velenovský 1889; Brown 1933; Krassilov 1973; Friis 1985*a*, *b*; Crane *et al.* 1986; Knobloch and Mai 1986; Manchester 1986; Friis *et al.* in press). In the mid-Cretaceous, inflorescences superficially resembling those of extant *Platanus kerrii* are associated with early platanoid foliage and provide some information on the organization of flowers and inflorescences in the early representatives of the group (Lesquereux 1892; Hickey and Doyle 1977; Dilcher 1979). Further details on floral structure are provided by three-dimensionally preserved inflorescences and flowers from the mid–late Albian of the Potomac Group, eastern North America that have been linked with platanoid foliage on the basis of field association and similarities in cuticular anatomy (Crane *et al.* 1986). Taken together, the information currently available from the mid-Cretaceous indicates that early platanoids resembled extant Platanaceae in having unisexual flowers clustered into globose heads, and were particularly like *P. kerrii* in possessing numerous sessile heads borne along a single inflorescence axis. These fossil plants however differed from the living taxa in the presence of five carpels per flower, the absence of hairs on the achenes, their well-developed perianth parts, and their small pollen. All of these features were apparently retained in some members of the platanaceous clade through the late Cretaceous and well into the early Tertiary (Friis 1984, 1985*b*; Manchester 1986) and probably reflect significant differences in reproductive biology. In particular the size of *in situ* pollen from Cretaceous and some early Tertiary forms is smaller than is typical of wind pollinated plants (Wodehouse 1935; Crane 1986) and suggests insect pollination (Manchester 1986; Crane *et al.*, 1986). The larger pollen and more reduced perianth of extant representatives, perhaps also *Platanites hebridicus*, may correlate with wind pollination (cf. Hesse 1978).

During the mid-Cretaceous palinactinodromous palmately lobed platanoid leaves intergrade in leaf architecture, venation, and cuticular structure with pinnatifid or pinnately compound foliage assigned to *Sapindopsis* (Doyle and Hickey 1976; Hickey and Doyle 1977; Upchurch 1984; Crane, in press *a*). Furthermore, preliminary work on mid-Cretaceous reproductive structures suggests that the inflorescences, flowers and pollen of platanoid and *Sapindopsis* plants were similar (Crane *et al.* 1986). *Sapindopsis* foliage has been interpreted as early evidence of the subclass Rosidae and the morphological similarities between platanoid and *Sapindopsis* plants have been used to infer a sister-group relationship between this subclass and the Hamamelidae (Wolfe *et al.* 1975; Doyle and Hickey 1976; Hickey and Doyle 1977; Crane, in press *a*; see also Cronquist 1981). This hypothesis receives further support from the leaves described in this paper. *P. hebridicus* significantly expands the foliar diversity known to occur within the platanaceous clade, clearly demonstrates the occurrence of pinnately compound leaves in the Platanaceae, and raises the question as to whether compound or simple leaves are basic within the group. The apparent absence of pinnately compound platanoid foliage during the late Cretaceous suggests that the leaves of *P. hebridicus* are specialized within the platanaceous clade, although the possibility that the compound condition reflects retention of a primitive character cannot be excluded. Resolving this question will be critical to interpreting the early radiation of non-magnoliid dicotyledons and will involve clarification of relationships within the mid-Cretaceous platanoid-*Sapindopsis* complex.

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